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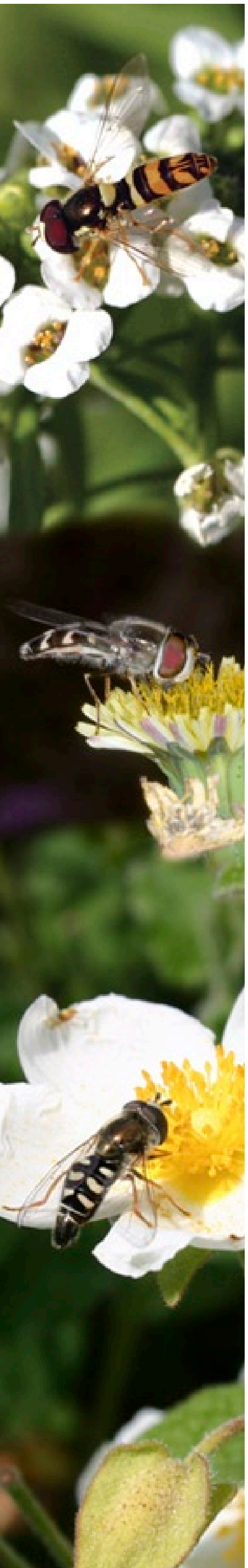

Flower Flies (Syrphidae) and Other Biological Control Agents for Aphids in Vegetable Crops

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Introduction

Biological control was originally defined as "the action of parasites, predators, or pathogens in maintaining another organism's population at a lower average than would occur in their absence" (DeBach 1964). Biological control is a key, though often underappreciated, component in agricultural pest management. In vegetable farming systems, various parasitic and predatory insects play important roles in reducing problems with aphids and other pests. Here we highlight aphid-feeding Syrphidae known as flower flies, also sometimes called hover flies or hoverflies.

California is the foremost producer of vegetable crops in the United States, with the top 34 crops accounting collectively for 863,000 planted acres, 847,000 harvested acres, and a value of $4,569,275,000 (2002 data). Principal production areas include the rich coastal flood plains of Monterey, San Benito, Santa Barbara, San Luis Obispo, and Ventura Counties; the desert of Imperial County; and Fresno, Kern, and Tulare Counties of the San Joaquin Valley (Monterey County Crop Report 2002; Santa Barbara County Crop Report 2002; Santa Cruz County Crop Report 2002; Ventura County Crop Report 2002).

Vegetables typically are produced in large-scale monocultures and often are produced on leased land—a disincentive for making changes with long-term payoffs but short-term costs. Vegetables also have short cropping periods with very quick turnaround between crops. There is a limited range of high-value rotational crops, although the moderate climates of coastal areas and many other parts of California permit year-round vegetable culture. Because of the high value of the land and the year-round favorable weather, there is little commercial use of low-value rotational crops or of cover crops that can be used to break pest cycles.

The large-scale monocultural production of vegetable crops enables growers to use low-cost seasonal labor and permits efficient mechanical and chemical weed control, fertilization, irrigation, and harvest. Destruction of alternate hosts for plant pathogens is a key element in managing viral problems in the Salinas

Valley (Wisler and Duffus 2000). Vegetable crops are short-statured, short-lived herbaceous plants, each of which begins life in the field as a seed or a transplanted seedling. Lettuce is grown continuously on the Central Coast of California, with planting beginning in January and ending in August. The crop is thinned about 30 days after planting and harvested at about 65 days. In comparison with tree and vine crops, vegetable crops are especially susceptible to competition from adjacent plants, whether these are other crops or weeds. For this reason, in-field plant diversity is often kept low in such systems, and opportunities for diversification are limited.

In light of the above conditions, pest and beneficial arthropods alike must either tolerate frequent disturbances or colonize rapidly from nearby or distant source areas and reproduce rapidly once they arrive. Key arthropod pests of vegetables in California include but are not limited to armyworms (*Spodoptera* spp.), cabbage looper *(Trichoplusia ni),* western flower thrips *(Frankliniella occidentalis),* western spotted cucumber beetle *(Diabrotica undecimpunctata* ssp. *undecimpunctata),* garden symphylan *(Scutigerella immaculata),* green peach aphid *(Myzus persicae),* lettuce aphid *(Nasonovia ribisnigri),* tarnished plant bug *(Lygus hesperus),* seedcorn maggot *(Delia platura)* (Hammond and Cooper 1993, Brust et al. 1997), and vegetable leafminer and its close relatives (*Liriomyza* spp.) (Palumbo et al. 1994). All of the above are subject to chemical applications (University of California IPM guidelines, http://www.ipm.ucdavis.edu/PMG). For romaine lettuce and most other lettuces, concerns over lepidopterous and aphid pests drive most of the use of carbamate and organophosphate insecticides.

Aphids present a special challenge to vegetable growers. Large numbers of winged, asexually reproducing females disperse from source areas and are borne on the wind to new infestation areas, including vegetable fields. These colonists produce a great number of progeny in a few days, and one female can produce a large infestation in a short time. In the Salinas Valley and neighboring areas, cabbage aphid *(Brevicoryne brassicae)* and green peach aphid *(Myzus persicae)* are important in cole crops. Bean aphid *(Aphis fabae)* is an important vector of viral pathogens to various crops. Lettuce aphid *(Nasonovia ribisnigri)* attacks all lettuce varieties. Melon aphid (= cotton aphid, *Aphis gossypii*) attacks cucurbits and cotton. Foxglove aphid *(Aulacorthum solani)* attacks lettuce and is often found in joint infestations with lettuce aphid, though lettuce aphid is generally present at high densities (Nebreda, Michelena, and Fereres 2005).

Lettuce aphid *(Nasonovia ribisnigri),* a pest of romaine lettuce that was introduced from Europe during the late 1990s, has proven particularly difficult to control (Parker et al. 2002). Lettuce aphid (asexually reproducing, live-bearing alate [winged] females: viviparae) colonizes romaine lettuce at any stage after emergence and infests the innermost leaves. The plants generally tolerate it well until they are thinned, about 20 to 30 days after planting. If natural enemies fail to suppress these early colonies, the aphids are thereafter protected because of the way the plant grows, with new leaves tightly packed together in the heart of the plant, limiting access by predators and parasites. Damage may result from aphid feeding and from the contamination of harvested portions of the lettuce with live aphids, exuviae, and honeydew. Washing prior to packing will remove some but not all of the contaminants. After the accidental introduction of the lettuce aphid into California, all lettuce growers were challenged to develop successful control programs, but organic growers faced special difficulties. Because most organically approved insecticides are ineffective against lettuce aphid, organic growers depend almost entirely on biological control (Chaney 2004; Colfer 2004).

Fortunately for farmers, aphids are attacked by several natural enemies including predators, pathogens, and parasites. Some types of natural enemies reside in the field and are already in place when the aphids arrive. Others can disperse rapidly and colonize shortly after the aphids become established. These natural enemies can reduce the aphid's rate of population increase or even wipe out infestations (Fig. 1). Biological control, mainly by aphidophagous flower flies (Syrphidae), typically leaves very little in the way of aphids, exuviae, or honeydew in the lettuce head. Plants remain clean if aphid densities do not become high and natural enemies eliminate lettuce aphid populations several days prior to harvest. In cases where many aphid exuviae and aphid cadavers (killed by entomopathogenic fungi) are left behind, the lettuce is harvested for processed romaine and the heads are divided and the leaves thoroughly washed.

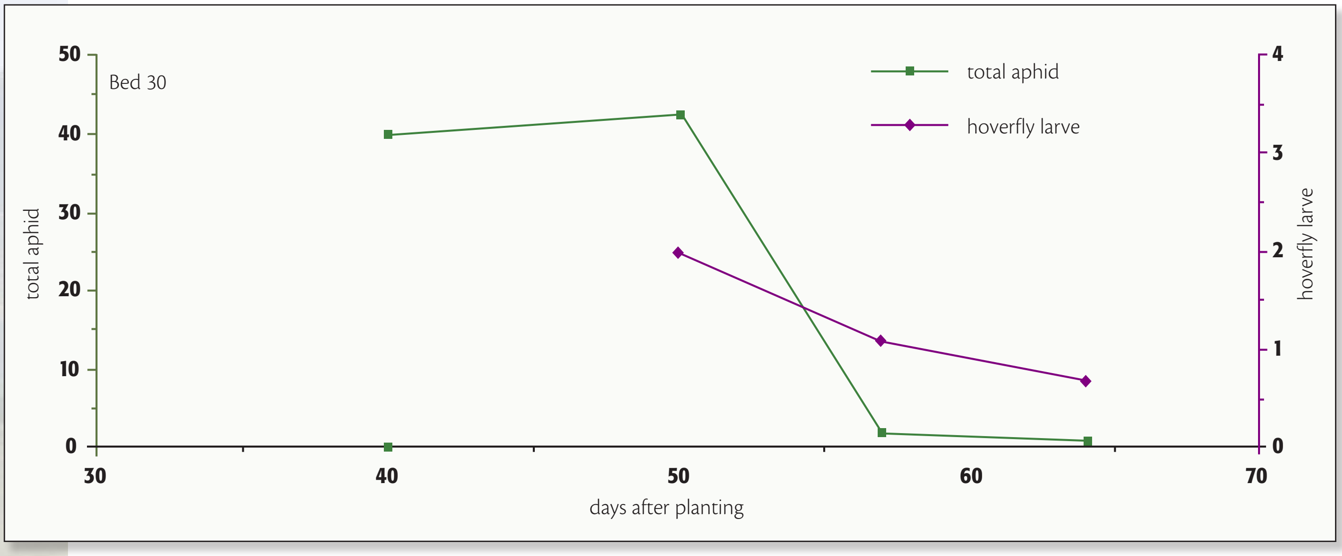

Figure 1. Lettuce aphids plant and aphidophagous flower fly (Diptera: Syrphidae) larvae per Romaine lettuce as functions of days after planting, Watsonville, Santa Cruz Co., CA, August, 2002. Data from other beds showed similar patterns (Franklin Dlott and William E. Chaney, unpublished data).

PREDATORS

The key natural enemies important in biological control, especially for lettuce aphid, are predators. Some of these predators have wide ranges of acceptable prey (generalists) and some have narrow prey ranges (specialists). Generalists include bigeyed bugs (*Geocoris* spp., Hemiptera: Lygaeidae) (Fig. 2, 3, 4, 5), damsel bugs (*Nabis* spp., Hemiptera: Nabidae), ground beetles (e.g., *Bembidion* spp., Coleoptera: Carabidae), brown lacewings (*Hemerobius pacificus, Hemerobius ovalis* [Fig. 6], and *Micromus* spp., Neuroptera: Hemerobiidae), green lacewings (*Chrysopa comanche, Chrysoperla carnea* [Fig. 7], and *Chrysoperla rufilabris,* Neuroptera: Chrysopidae), and minute pirate bug (*Orius tristicolor,* Hemiptera: Anthocoridae). These generalist predators prey not only on aphids, but also on mites, thrips, and eggs of moths and butterflies. On seedling crops, bigeyed bugs and ground beetles can easily be observed foraging on the soil surface and on the young plants, attacking small arthropods that they encounter. Several studies indicate that these generalists can prevent aphid outbreaks or reduce rates of population increase (Tamaki 1972; Tamaki and Weeks 1972; Tamaki 1981;Tamaki, Annis, and Weiss 1981). However, once an aphid outbreak occurs, generalists appear to be less effective than specialized natural enemies.

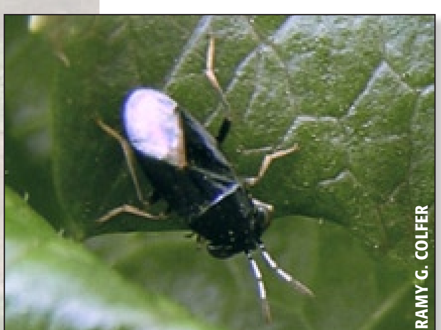

Figure 2. *Geocoris atricolor* adult on romaine lettuce.

Figure 3. Big-eyed bug (*Geocoris pallens*) attacking egg mass of beet armyworm (*Spodoptera exigua*) on leaf of bell pepper plant.

Figure 4. Nymph of big-eyed bug (*Geocoris pallens*) attacking nymph of another species of big-eyed bug (*Geocoris punctipes*) on stem of cotton plant.

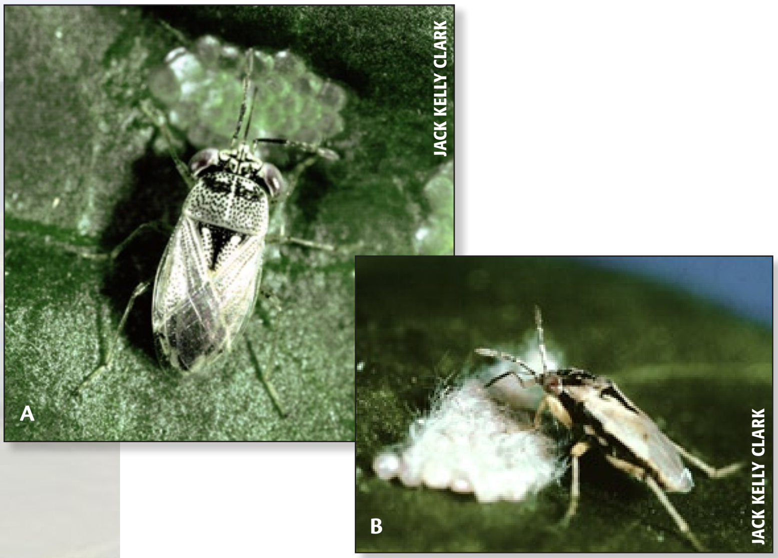

Figure 5. (A) Big-eyed bug *(Geocoris punctipes)* attacking egg mass of omnivorous leafroller *(Platynota stultana)* on leaf of bell pepper plant and (B) attacking egg mass of beet armyworm *(Spodoptera exigua)* on leaf of bell pepper plant.

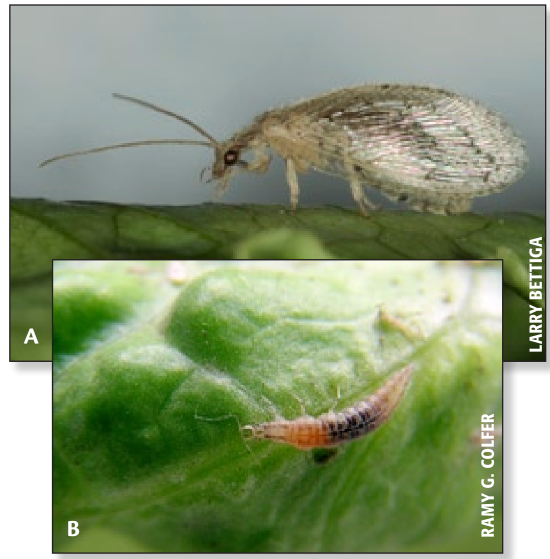

Figure 6. (A) Adult brown lacewing *(Hemerobius ovalis)* on lettuce leaf. (B) Larva of brown lacewing (*Hemerobius* spp.) on romaine lettuce.

Predators that focus mainly on aphids include lady beetles (*Hippodamia convergens* [Fig. 8, 9], *Coccinella novemnotata, Coccinella septempunctata* [Fig. 10], and others, Coleoptera: Coccinellidae), aphid midge (*Aphidoletes aphidimyza,* Diptera: Cecidomyiidae), and flower flies (Diptera: Syrphidae), also called hover flies or hoverflies.

The relative importance of different predators varies with location and season. *Coccinella novemnotata* and aphid midge are seldom seen in cool-season vegetables, whereas *Coccinella septempunctata* seems to be becoming increasingly abundant and brown lacewing larvae are able to forage efficiently inside the romaine head. However, on California's Central Coast it is primarily syrphid larvae that enable organic lettuce growers to produce harvestable crops (Smith and Chaney 2007).

Several studies show that individual contributions by members of a "guild" of natural enemies that attack aphids may not always be cumulative and may not always lead to improved biological control. For example, based on data from cage studies with cotton aphid *(Aphis gossypii),* common green lacewing *(Chrysoperla carnea)* is a viable control agent by itself, but intraguild predation on *C. carnea* larvae by predatory true bugs (Heteroptera), especially the assassin bug *(Zelus renardi),* interferes with this potential biological control (Rosenheim, Wilhoit, and Armer 1993; Rosenheim, Limburg, and Colfer 1999). Predation on lacewing larvae by damsel bugs (*Nabis* spp.) and bigeyed bugs (*Geocoris* spp.) has smaller deleterious effects. Jay Rosenheim (pers. comm.) emphasized that although predatory true bugs may interfere with biological control of cotton aphid, they are nonetheless key in controlling pest Lepidoptera and spider mites. Thus, there can be trade-offs. By contrast with work by Rosenheim and colleagues, Dinter (2002) demonstrated in small enclosures with wheat that dwarf spiders preyed on larvae of the common green lacewing but that this predation did not interfere with biological control of grain aphids. Also, the presence of alternative prey (e.g., vinegar fly, *Drosophila melanogaster,* Diptera: Drosophilidae) lessened intraguild predation and did not interfere with overall biological control of aphids.

Biological control agents may also be attacked by parasites. For example, occasionally there is high incidence (nearly 60%) of parasitism of syrphid larvae (Smith and Chaney 2007) by parasitic wasps such as *Diplazon* sp. (Hymenoptera: Ichneumonidae or *Pachyneuron* sp. (Hymenoptera: Pteromalidae).

Movement by arthropods varies not only among species, but also seasonally (Corbett 1998), sometimes including long-distance dispersal before and after overwintering. Beneficial arthropods may colonize vegetable fields by dispersing from habitat in wildlands, hedgerows, weedy areas, or agricultural fields. For

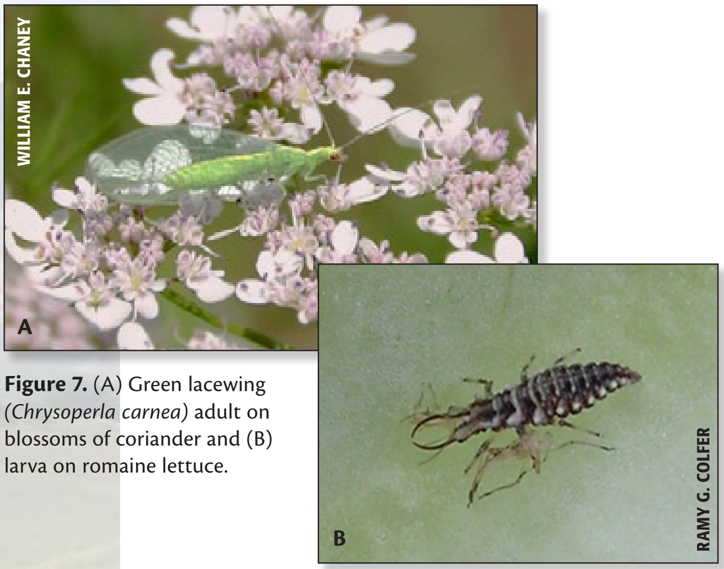

Figure 7. (A) Green lacewing *(Chrysoperla carnea)* adult on blossoms of coriander and (B) larva on romaine lettuce.

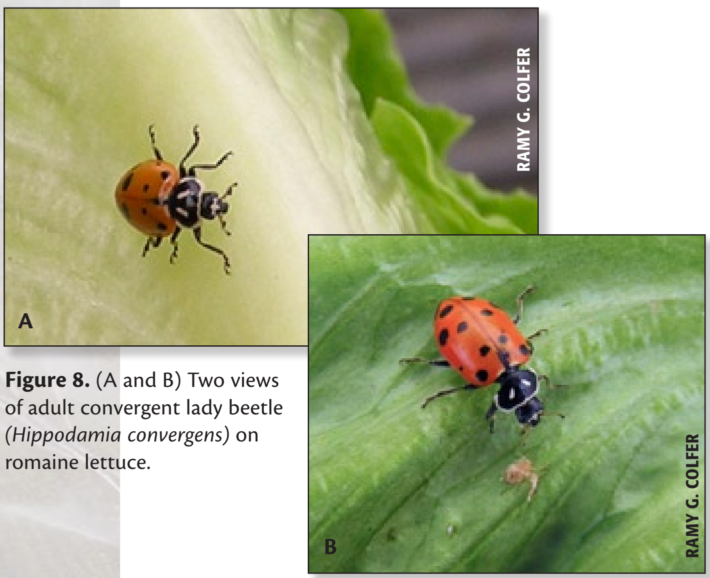

Figure 8. (A and B) Two views of adult convergent lady beetle *(Hippodamia convergens)* on romaine lettuce.

Figure 9. Larva of convergent lady beetle *(Hippodamia convergens)* on romaine lettuce.

example, bigeyed bugs (*Geocoris* spp.) overwinter amid field-side weeds and in alfalfa fields and fly to vegetable fields in early spring. By contrast, immature dwarf spiders spin silk and are wafted by the wind, thereby "ballooning" in several successive events to colonize new sites (Weyman, Sunderland, and Jepson 2002; Thomas, Brain, and Jepson 2003). Subsequent dispersal between fields may also occur during the growing season. Dwarf spiders prey on cereal aphids (Bilde and Toft 2001) and are expected to build up in and disperse from cover crops that include cereal grains.

Predators and parasites colonize vegetable fields from other fields and from field-side weeds and more distant vegetation. Regardless of their mode of colonizing, beneficial arthropods require resources once they arrive in vegetable fields, and fields of tilled soil with tiny seedling crops may not, by themselves, suffice. Many predatory and parasitic arthropods feed not only on arthropod pests but also on nectar, pollen, and alternate hosts and prey that may be afforded by non-crop plants. Where such plants are encouraged or tolerated with these functions in mind, they are called "insectary plants."

Larvae of several flower fly species feed on aphids; these are termed aphidophagous flower flies, and all are in the subfamily Syrphinae. Common aphidophagous flower flies in California vegetable crops include *Toxomerus marginatus, Platycheirus stegnus, Sphaerophoria sulphuripes, Allograpta obliqua, Syrphus opinator, Eupeodes volucris, Toxomerus occidentalis,* and *Paragus tibialis.* Other aphidophagous species found feeding in lettuce aphid in California include *Scaeva pyrastri, Eupeodes americanus, Sphaerophoria contigua, Sphaerophoria pyrrhina, Platycheirus obscurus,* and *Allograpta exotica.*

European studies under greenhouse conditions suggest that common green lacewing *(Chrysoperla carnea)* may be a useful biological control agent for lettuce aphid, but that parasites are less valuable (Quentin, Hommes, and Basedow 1995). Central Coast data from UC Cooperative Extension Farm Advisor William Chaney and colleagues indicate that parasites and lacewings are not important in the control of this aphid. However, data from Watsonville (Santa Cruz County) and Spreckels (Monterey County) have repeatedly shown that other predators are important, particularly aphidophagous flower flies (Diptera: Syrphidae), which can almost eliminate lettuce aphid by the time of harvest. The most common flower fly species observed were these small species: *Toxomerus* *marginatus, Platycheirus stegnus, Sphaerophoria sulphuripes* and *Allograpta obliqua.* Other larger species that are commonly seen in commercial romaine lettuce on the Central Coast include *Eupeodes americanus* and *Eupeodes volucris.*

Syrphidae

Overview

Flower fly development involves complete metamorphosis, including egg (Fig. 11), three larval stages, puparium, and adult. Adults of many flower fly species resemble stinging bees and wasps. This phenomenon is called Batesian mimicry, indicating that palatable organisms resemble or "mimic" unpalatable models. Worldwide, there are many aphidophagous syrphid species. For example, at least 49 species of Syrphidae attack green peach aphid, *Myzus persicae* (Van Emden et al., 1969). Adult aphidophagous Syrphidae often visit flowers, and the shapes of their mouthparts suggest that some species mainly feed on nectar, whereas others also take pollen (Gilbert 1981). Adult hover flies require honeydew or nectar and pollen to ensure reproduction, whereas larvae usually require aphid feeding to complete their development (Schneider 1969). However, there are exceptions: in the absence of aphids, larvae of some species can subsist and complete development on diets made up solely of plant materials such as pollen (e.g., *Melanostoma* and *Allograpta obliqua* [Schneider 1969] and *Toxomerus* [*Mesograpta* sp.] [Cole and Schlinger 1969]).

Adult syrphids can be sampled by several methods, including visual scanning of crops while walking, aerial netting, and using suction traps, Malaise traps, or water traps. For assessing eggs, larvae, and pupae of aphidophagous Syrphidae, removal of whole plants from the field and examination in the laboratory proved superior to both quick inspection of plots (while walking) and detailed visual inspection of plants in the field (Lapchin et al. 1987).

Figure 10. (A) Adult seven-spotted lady beetle *(Coccinella septempunctata)* on romaine lettuce. (B) Seven-spotted lady beetle larva on romaine lettuce.

Figure 11. Syrphid egg on romaine lettuce.

Figure 12. Adult female *Allograpta obliqua.*

Figure 13. Adult male *Allograpta* sp. on inflorescence of sweet alyssum (*Lobularia maritima*).

Figure 14. (A and B) Two views of *Allograpta obliqua* larvae on romaine lettuce.

Some of the aphidophagous syrphids most common in California are as follows (adapted from Metcalf 1911a, 1911b, 1912a, 1912b, 1913; Heiss 1938; Bugg 1992; and Láska et al. 2006):

1. The adult chevroned Allograpta fly, *Allograpta obliqua* (Say) (Fig. 12, 13), is about 0.85 cm or less in length, and slenderer than *E. volucris*. The face is yellow, lacking a complete medial stripe. This species has transverse yellow bands on the abdomen, and two oblique yellow marks near the tip. The larvae (Fig. 14) are 0.9 – 1.1 cm long, and are smooth and green, with a broad, white median strip. The breathing tubes are prominent. Other *Allograpta* spp. may also be encountered, including *Allograpta exotica* (Wiedemann). Figure 15 shows an adult dark morph of *Allograpta* sp.

2. The adult American flower fly, *Eupeodes americanus* (Wiedemann) (Fig. 16), is similar to S. opinator, is 0.9 to 1.2 cm long, but has black vitta (stripes) on the face, including a stripe down the front, and its thorax is shiny. Larvae (Fig. 17) are about 1.1 cm long and are yellowish or salmon brown, marked with black and white or yellowish white. The whitish markings consist of a transverse rectangular bar on each segment from 6 to 11 and a narrow line along each side of the larva in the dorsal lateral carinas. The heartline or dorsal blood vessel appears as 6 wedge-shaped black marks broadly margined with brown. The larvae of this species are especially active; early instars have visible black setae.

3. The adult Eupeodes flower fly (*Eupeodes volucris* Osten Sacken [Fig. 18, 19]) female looks similar to the Scaeva flower fly, but is only 0.85 to 1.00 cm long; the face is whitish yellow with black cheeks and a dark medial stripe; and males have a narrow cylinder at the tip of the abdomen. The larva (probably Fig. 20) is 0.9 to 1.4 cm long and moderately spiny and is greenish with dorsal streaks of soft pink and white, yellow and white, or green and white. The dorsum is bounded laterally by two narrow, irregular white lines that follow the ridge of the dorso-lateral segmental bristles.

Figure 15. Adult dark morph of *Allograpta* sp.

Figure 16. Adult male *Eupeodes americanus.*

Figure 17. (A) Larva of *Eupeodes americanus* on romaine lettuce and (B) with cabbage aphid (*Brevicoryne brassicae*) on broccoli.

Figure 18. Adult female *Eupeodes volucris.*

Figure 19. Adult male *Eupeodes volucris* on rockrose (*Cistus* sp.) flower.

Figure 20. Syrphid larva, probably *Eupeodes volucris,* on romaine lettuce.

Figure 21. Adult female *Paragus tibialis.*

Figure 22. Adult male *Paragus tibialis.*

4. Adult *Paragus tibialis* (Fallen) (Fig. 21, 22) are small, 0.3 to 0.5 cm long, and have a rounded posterior abdomen. The face is light yellow and yellow on the sides with a broad median black band from antennae to oral margin. The abdomen of the male is reddish brown, whereas that of the female may be either reddish brown or greenish black. The larval length is about 0.75 cm, width 2 to 2.5 mm, and height 1.5 mm, with color ranging from yellow to light yellow brown.

5. Adult *Platycheirus* spp. (Fig. 23) are about 1.0 to 1.1 cm in length and dark colored with subtle silver or tan markings on the abdomen. The face is silver to dark gray to black. These are the only species that commonly lay eggs in parallel, contiguous clusters. The larvae (Fig. 24) are 1.0 to 1.2 cm long and are tan to orange. These species are likely to be found on plants with high aphid densities (Smith and Chaney 2007).

6. The adult Scaeva flower fly, *Scaeva pyrastri* (L.) (Fig. 25) adults are 1.27 cm in length. The face is white with dark medial vitta (stripes). The abdomen is dark with six white, curved stripes. Larvae (Fig. 26) are 1.2 to 1.8 cm long and light green with a white dorsal longitudinal stripe.

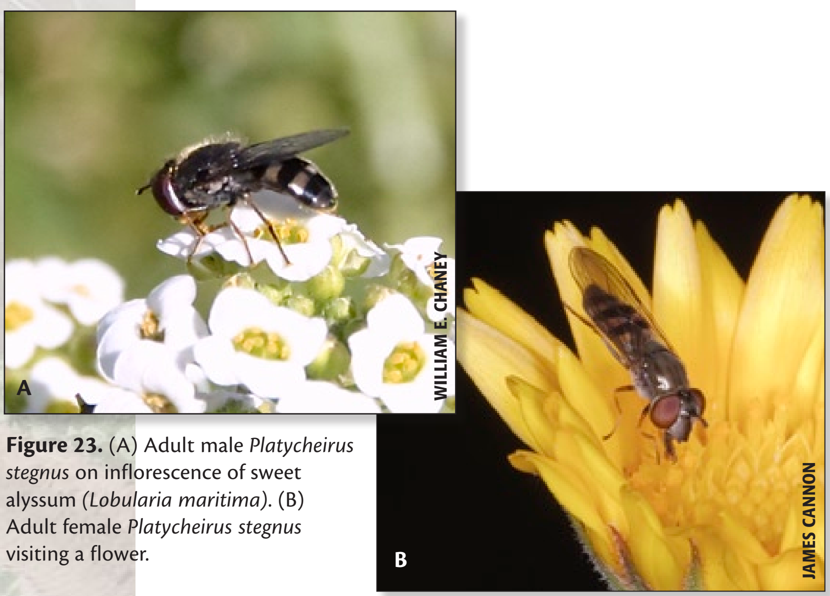

Figure 23. (A) Adult male *Platycheirus stegnus* on inflorescence of sweet alyssum *(Lobularia maritima)*. (B) Adult female *Platycheirus stegnus* visiting a flower.

Figure 24. Larva of *Platycheirus stegnus* on romaine lettuce.

7. Adult *Sphaerophoria* spp. (Fig. 27) are about the same size as *Allograpta obliqua,* with a body length about 0.85 cm, but with a narrow, cylindrical abdomen. The face is white or yellow and may have a medial black stripe (as with *Sphaerophoria sulphuripes* [Thompson]). The larvae (Fig. 28) are about 1.0 cm long, greenish yellow, and more or less transparent.

8. The adult western Syrphus fly, *Syrphus opinator* Osten Sacken (Fig. 29) adult is 0.7 to 1.2 cm long, has a yellow face, and has two black spots and two bands extending across the abdomen. The larvae (Fig. 30) are about 1 to 1.3 cm long and are spiny and yellow or brown.

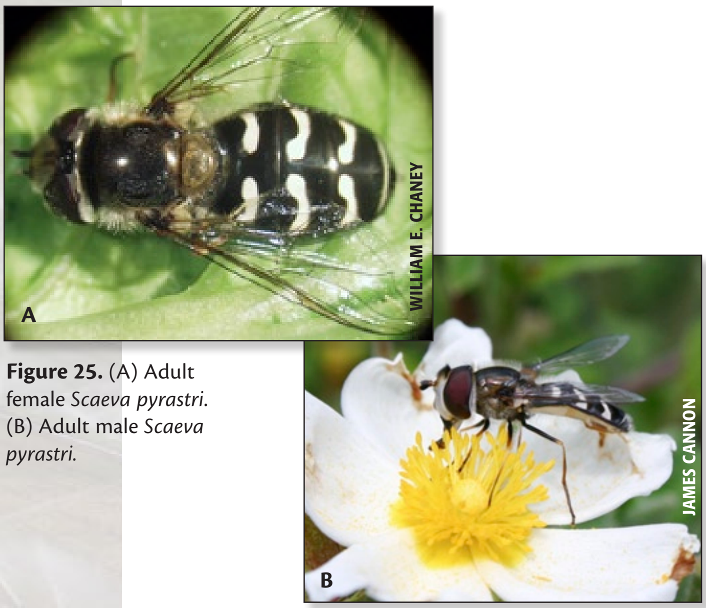

Figure 25. (A) Adult female *Scaeva pyrastri.* (B) Adult male *Scaeva pyrastri.*

Figure 28. Larva of *Sphaerophoria sulphuripes* on romaine lettuce.

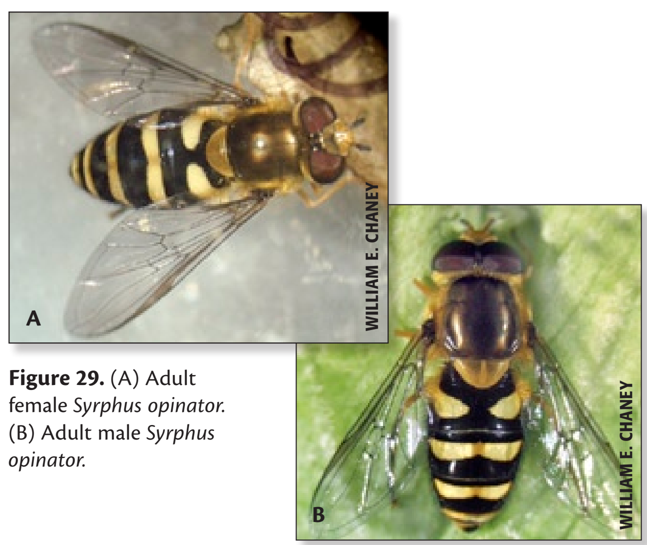

Figure 29. (A) Adult female *Syrphus opinator.* (B) Adult male *Syrphus opinator.*

Figure 26. Larva of *Scaeva pyrastri* on romaine lettuce.

Figure 27. Adult female *Sphaerophoria sulphuripes.*

Figure 30. Larva of *Syrphus opinator* on romaine lettuce.

9. Adult *Toxomerus* spp. are small, rounded flies with dark markings on the margins of the abdomen. Body length for *Toxomerus marginatus* (Say) (Fig. 31) is 0.5 to 0.6 cm; for *Toxomerus occidentalis* (Curran) (Fig. 32), 0.6 to 0.75 cm. Males of the latter species have distinctive enlarged hind femurs. The face of *T. marginatus* is yellow; the female forehead is dark with lateral yellow stripes. The face of *T. occidentalis* is white, but the forehead is dark. Larvae (Fig. 33) are 0.4 to 0.45 cm long, translucent, and cream colored, and have a visible gastrointestinal system colored by their food source. This group is more likely than others to lay eggs on plants when very low numbers of aphids, or even no aphids, are present (Smith and Chaney 2007).

Common non-aphidophagous syrphids on Californian farmlands include *Eristalis* spp. (Fig. 34) and *Helophilus* spp. (Fig. 35), known as rat-tailed maggots due to their long, tubular tails, the larvae of which live in liquified manure or in sewage ponds; *Eumerus* spp. (Fig. 36), the larvae of which feed on the bulbs of plants; and *Syritta pipiens* (Fig. 37), the adults of which have distinctive enlarged hind femurs and the larvae of which have very short tails and live in manure or rotting organic matter. To the untrained eye, adults of these species may resemble the aphid predators.

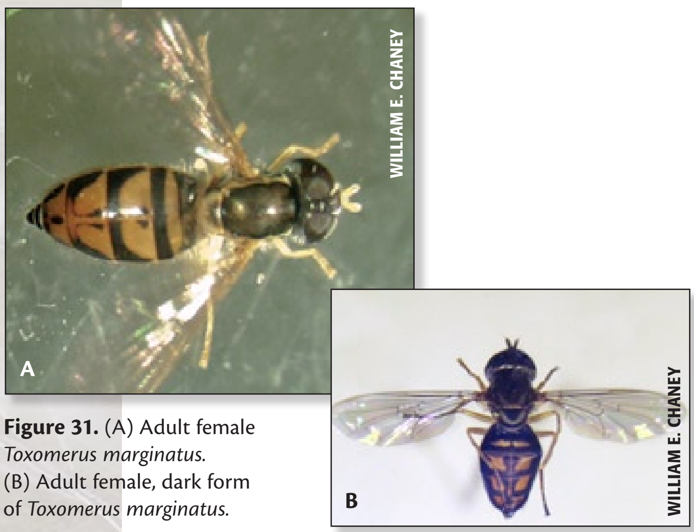

Figure 31. (A) Adult female *Toxomerus marginatus*. (B) Adult female, dark form of *Toxomerus marginatus*.

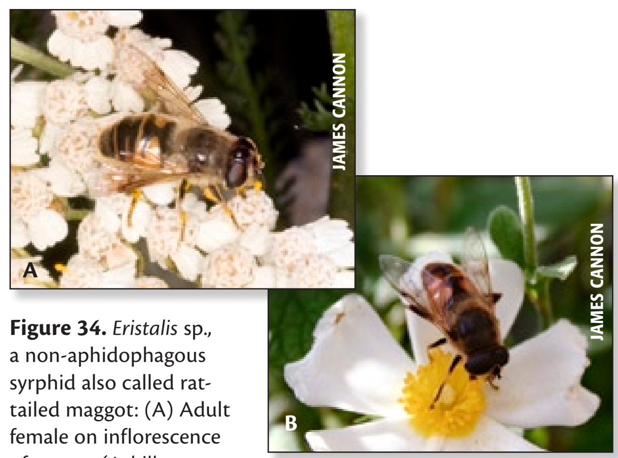

Figure 34. *Eristalis* sp., a non-aphidophagous syrphid also called rat-tailed maggot: (A) Adult female on inflorescence of yarrow (*Achillea millefolium*). (B) Adult *Eristalis* sp. on rock rose (*Cistus* sp.).

Figure 32. Adult female *Toxomerus occidentalis*.

Figure 33. Larva of *Toxomerus marginatus* on romaine lettuce.

Figure 35. Adult *Helophilus* sp., a non-aphidophagous syrphid.

Figure 36. Adult *Eumerus strigatus* (Fallén), a non-aphidophagous syrphid.

Figure 37. Adult *Syritta pipiens* (L.), a non-aphidophagous syrphid, at flower of rockrose (*Cistus* sp.)

Aphidophagous Syrphid Behavior

Aphid colonies may last only a few days: they can appear quickly and just as suddenly disappear due to predation, parasitism, fungal epizootics, declining host-plant quality, changes in weather, or dispersal. Therefore, predators must be quick to locate aphid infestations. Because they are strong fliers and able to hover and inspect foliage for aphids, syrphids may be especially good at locating aphid colonies. Syrphids may be better at locating aggregations of aphids on collards than are Coccinellidae (Coleoptera) or Chrysopidae (Neuroptera) (Horn 1981).

Adult aphidophagous syrphids are high-performance insects and, although they are strong fliers, are mainly inactive when weather is cold, wet, or windy (Lewis 1965a). In the Sacramento Valley, the larger species *Eupeodes* spp., *Scaeva pyrastri,* and *Syrphus* spp. are often abundant from late spring through early summer, but seem to disappear from open fields with the onset of summer heat. Some large species may still be found in cool, shady areas during summer. In coastal areas, the larger species often remain abundant during the summer (Bugg, pers. observation). By contrast, the smaller *Toxomerus* spp. and *Paragus tibialis* (Fallen) are most common during summer, in both warm interior valleys and cool coastal areas (Bugg and Wilson 1989).

On the Central Coast in the fog belt, lettuce aphid biological control generally is less effective during periods of cool, cloudy weather. Also, growth chamber studies by one of us (W. E. C.) have shown that lettuce aphids reproduce more rapidly at lower temperatures. Corroborating these laboratory observations, another of us (R. G. C.) has found that the worst lettuce aphid problems have always occurred during cool spring conditions or prolonged cool/foggy periods during the summer. Syrphid larval activity appears to vary tremendously from day to day, depending on the temperature.

Adult females of several syrphid species determine whether to oviposit based on the size of aphid colonies**.** Several syrphid species discriminate against older, larger colonies in favor of smaller “promising” colonies (Kan 1988a, b, c). However, syrphid species vary as to the size of the aphid colonies or aggregations they select. Chandler (1968a) showed that, for *Platycheius* spp. and *Syrphus ribesii* (L.), different aphid densities elicited peak numbers of syrphid eggs per plant. Chandler (1968b) also reported that *Platycheirus manicatas* (Meigen) oviposited selectively on uninfested plants adjoining those that were heavily infested. This behavior was observed in response to cabbage aphid (*Brevicoryne brassicae* L.) on brussels sprouts and to bean aphid (*Aphis fabae* Scopoli) on faba beans. In California, Hugh Smith and William E. Chaney found that *Toxomerus* spp. oviposit on plants that have been poorly colonized by aphids and may be especially good at keeping aphids at low densities.

Managing Vegetation to Enhance Biological Control by Syrphidae

Cover crops, windbreak and hedgerow plants, cut flowers, culinary herbs, and some weeds can be important in managing flower flies. These plants can modify microclimates and provide foods, including pollen, nectar, and alternate prey. These provide both nectar to meet the high energy requirements of flight and pollen to sustain egg production (Schneider 1969), and also provide alternate prey, wind shelter, and possibly overwintering habitat for flower flies.

Adult syrphids seldom fly in strong winds. Hedgerows, windbreaks, or shelterbelts can protect croplands in windy areas. They can provide protection to a limited distance on their windward sides and to greater distances on their leeward sides. Shelter can reduce soil erosion, improve the photosynthetic and water-use efficiency of crop plants, and lead to locally elevated temperatures in the sheltered areas (Van Eimern 1964). All of this means that wind shelter is a factor that may be used to enhance biological control by aphidophagous syrphids. Several studies have shown that adult aphidophagous syrphids aggregate in sheltered zones (Lewis 1965a; Pollard 1971; Lovei, Macleod, and Hickman 1998).

Only preliminary observations and survey studies have been conducted on the possible role of alternate prey in enhancing biocontrol by syrphids. Early observations suggest that some hedgerow plants sustain aphids and associated flower flies that may be valuable in the biological control of vegetable pests. Promising hedgerow plants include California honeysuckle *(Lonicera hispidula),* which hosts honeysuckle aphid (*Hyadaphis tataricae*), California coffeeberry *(Rhamnus californica* ssp. *californica),* which hosts *Macrosiphum rhamni*, and various California lilacs (*Ceanothus* spp.) that host *Aphis ceanothi* (R. L. Bugg, pers. observation).

Bugg and Dutcher (1989) evaluated several warm-season cover crops as sources of alternate prey for aphidophagous insects, with *Sesbania exaltata* harboring the highest densities of Syrphidae. Bugg, Phatak, and Dutcher (1990) assessed adult aphidophagous Syrphidae in various cool-season cover crops in southern Georgia. They observed *Allograpta obliqua*, *Syrphus* sp., *Eupeodes (Metasyrphus)* sp., and *Toxomerus marginata*. Whole-plot inspection for pooled adult aphidophagous syrphids indicated significant differences among cover crops on 5 of the 19 sampling dates. Thus, significant differences for adult aphidophagous Syrphidae were seen only on a relatively few occasions. Adult syrphids seldom fly when the weather is windy, cold, or rainy, and they may seek concealed locations under these conditions. Therefore they may not have been observable on all sampling dates.

Bugg and Ellis (1990) evaluated five cover crops grown during the summer in Falmouth, Massachusetts: bell bean, buckwheat, hairy vetch, sorghum, and white sweetclover. These workers observed at least four species of aphidophagous flower flies. Among 725 syrphid adults, there were 658 *Toxomerus* spp. (over 90%), 55 *Sphaerophoria* spp., 9 *Syrphus* spp., and 3 *Allograpta obliqua.* During weekly sampling, buckwheat (a nectar source) showed the highest densities on three dates; hairy vetch *(Vicia villosa)* (infested with pea aphid [*Acyrthosiphon pisum*]) did so on two dates.

Insectary hedgerows of perennial woody trees and shrubs are occasionally used on California's Central Coast. Windbreaks have long been used to shelter crops on the Central Coast. Blue gum *(Eucalyptus globulus)* has been used since the 1880s, flowers in the winter, and attracts aphidophagous syrphids. Athel *(Tamarix aphylla)* flowers in the summer and attracts various predatory insects. Other tree species in older windbreaks have little apparent value as insectaries. Insectary plants suitable for hedgerows include black sage *(Salvia mellifera),* California buckwheat *(Eriogonum fasciculatum),* California lilac (*Ceanothus* spp.), white sage *(Salvia apiana),* willows (*Salix* spp.), goldenrods *(Euthamia occidentalis, Solidago californica),* heliotrope *(Heliotropium curassavicum),* yarrow *(Achillea millefolium),* and other sources of nectar, pollen, and alternative prey and hosts (see Bugg et al. 1998; Dufour 2000; Earnshaw 2004).

Many organic growers plant insectary crops with the intention of enhancing syrphid activity in lettuce. Insectary crops are flowering plants that provide floral resources, primarily nectar and pollen, to syrphid adults and other beneficial insects. Sweet alyssum *(Lobularia maritima)* and coriander *(Coriandrum sativum)* are commonly used insectary crops in Central Coast organic farming (Fig. 38). There is much variation in the use of insectary crops among organic producers on the Central Coast. Some growers interplant a few complete beds of alyssum at intervals across a lettuce field. Others plant a single seed line of alyssum, cilantro, or a "good bug blend" spaced among a certain number of beds. Some organic growers prefer to intersperse individual plants of alyssum and cilantro in the field rather than plant it in rows, while others plant stands of mustards and fennel (Fig. 39) as insectary crops instead of interplanting insectary crops in rows. Some insectary plantings may also harbor pests or result in weed problems. Habitat manipulations also have an economic cost. The land devoted to insectary plantings is lost to cash crops, and this may amount to 10 percent of the arable acreage. There are also costs incurred in planting and maintaining insectary plants. In the absence of formal studies, it is still uncertain whether this opportunity cost is offset by improved pest control.

Most large, successful organic lettuce growers use the approach, so the opportunity costs and other costs appear to be tolerable.

Some culinary herbs and cut flowers have a high potential value as insectary plants. Such plants can also be harvested to offset costs. Culinary herbs that attract abundant syrphids include lemon verbena *(Lippia [=Aloysia] citriodora),* oregano *(Origanum vulgare)* (Wäckers 2004), common culinary sage *(Salvia officinalis),* culinary thyme *(Thymus vulgaris)* (Müller 1883), and spearmint *(Mentha spicata)* (Maingay et al. 1991; Al-Doghairi and Cranshaw 1999) and some varieties of rosemary *(Rosmarinus officinalis)* (e.g., 'Blue Spires' and 'Miss Jessup'). In the mild Mediterranean climate of the Central and Gold Coasts of California, most of these plants can be grown as perennials, although culinary thyme only has a span of about 3 years. Several of these herbs are typically harvested before flowering, but gourmet chefs actually prefer them when in flower. Cut flowers that attract syrphids include angelica *(Angelica archangelica),* annual baby's breath *(Gypsophila muralis),* bishop's weed *(Ammi majus),* coxcomb *(Celosia cristata),* Queen Anne's Lace *(Daucus carota),* California native wild buckwheats (especially *Eriogonum grande* var. *rubescens, Eriogonum giganteum,* and *Eriogonum latifolium* var. *rosea*), annual clary sage (*Salvia horminum* var. 'Marble Arch'), and yarrow (*Achillea millefolium,* especially white, pink, and red varieties).

Common agricultural and roadside weeds may serve as floral or aphid sources, but they have been the focus of very limited formal research in these roles. Floral sources include chickweed *(Stellaria media),* corn spurry *(Spergula arvensis),* dove mullein *(Eremocarpus setigerus),* knotweeds and smartweeds (*Polygonum* spp.), shepherd's purse *(Capsella bursa-pastoris),* poison hemlock *(Conium maculatum),* various spurges (Eurphorbiaceae), wild carrot *(Daucus carota),* wild fennel *(Foeniculum vulgare),* and wild mustards (*Brassica* spp.). Aphid sources include annual sowthistle *(Sonchus oleraceus),* knotweeds (*Polygonum* spp.), pineapple weed *(Matricaria discoidea),* stinking chamomile *(Anthemis cotula),* wild mustards, and various winter-annual grasses.

Figure 38. (A) Sweet alyssum *(Lobularia maritima)*. (B) Insectary plantings of sweet alyssum and cilantro (coriander), interspersed with organic romaine lettuce. (C) Insectary plantings of sweet alyssum, interspersed with organic romaine lettuce. (D) Insectary mix of sweet alyssum and barley *(Hordeum vulgare)* in a commercial organic lettuce field, Imperial County, California.

Figure 39. Sweet fennel *(Foeniculum vulgare)* in organic broccoli field.

Figure 40. Persian clover (*Trifolium resupinatum* ssp. *resupinatum,* cv. 'Nitro').

Table 1 lists some of the nectar sources used by aphidophagous syrphids, including trees, shrubs, and forbs. The table refers to research conducted in both North America and Europe. As indicated in Table 1, flowers of some cover crops such as buckwheat *(Fagopyrum esculentum,* Polygonaceae) and tansy phacelia (*Phacelia tanacetifolia,* Hydrophyllaceae) are especially attractive to adult syrphids (Ozols 1964). Sweet alyssum *(Lobularia maritima,* Brassicaceae) flowers are also heavily visited (Bugg, pers. observation), and this species is commonly included in proprietary "insectary cover crop" seed mixes (e.g., Germain's Incorporated, Harmony Farm Supply, Lohse Mill Inc., Pacific Coast Seed, Peaceful Valley Farm Supply) (Bugg and Waddington 1994). Persian clover (*Trifolium resupinatum* var. *majus*, cv. 'Lightning') (Fig. 40) is a soft-seeded variety of a species that is highly attractive to flower flies. This form is less likely to become a persistent weed than are hard-seeded varieties (*Trifolium resupinatum* var. *resupinatum*, e.g., cv. 'Nitro').

Oviposition by syrphids appears to be influenced by wind shelter and by the presence of flowers. It may be difficult to demonstrate the flowers' effects on biological control because of difficulties that are both spatial and temporal in nature: adult syrphids are highly mobile, a characteristic that is enhanced when they feed on an energy food such as nectar, and the benefits that they appear to derive from pollen feeding (e.g., ovariole development) do not become apparent until some time after feeding.

The distribution pattern of syrphid flies and their oviposition on brussels sprouts were ascribed to the effects of flowers in a study involving a hedgerow (Van Emden 1965). Pollard (1971) contended that the shelter provided by hedges was important, but that flowers were not. Both of these studies were unreplicated, however.

By contrast, Şengonça and Frings (1988) showed apparent enhancement of biocontrol in a two-year replicated study involving tansy phacelia. This annual forb is native to California and was introduced to Europe as a bee plant during the early 1900s. Tansy phacelia was grown in interior strips and in "islands" in conjunction with 200 m^2 plots of sugarbeet. Hover flies with the distinctive star-shaped phacelia pollen in their guts were collected as

Table 1. Flowering plants and associated aphidophagous flower flies (Diptera: Syrphidae)

Nectar source	Plant growth habit, seasonality, and uses in agriculture	Syrphidae attracted	References
Baby's breath *(Gypsophila grandiflora)* 'Covent Garden'	Cut flower	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Buckwheat *(Fagopyrum esculentum)*	Herbaceous summer annual, warm-season cover crop	*Allograpta obliqua, Ocyptamus costatus, Ocyptamus fuscipennis, Pseudodoros clavatus, Toxomerus boscii, Toxomerus marginatus* *Syrphus opinator, Sphaerophoria sulphuripes*	Bugg and Dutcher 1989 W. E. Chaney, pers. obs.
Buckwheat and canola *(Brassica napus)*	Herbaceous broadleaf annuals, cover crops	*Allograpta obliqua, Sphaerophoria* spp., *Syrphus* spp., *Toxomerus* spp.	Bugg and Ellis 1990
California lilacs *(Ceanothus* spp.)	Woody perennial: shrub, insectary hedgerows, chaparral plant	*Allograpta obliqua, Sphaerophoria* spp., *Scaeva pyrastri, Eupeodes volucris, Eupeodes* spp., *Melanostoma* sp., *Toxomerus* spp. *Syrphus opinator*	Bugg, pers. obs. W. E. Chaney, pers. obs.
California poppy *(Eschscholzia californica)*	Herbaceous broadleaf, wildflower	*Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Common Coriander *(Coriandrum sativum)*	Herbaceous annual, culinary herb or spice, insectary plant	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Common knotweed *(Polygonum aviculare)*	Annual, prostrate broadleaf weed on roadsides	*Allograpta* spp., *Sphaerophoria* spp., *Paragus tibialis*	Bugg, Ehler, and Wilson 1987
Corn spurry *(Spergula arvensis)*	Annual broadleaf weed in acid soils	*Allograpta obliqua, Eupeodes volucris, Melanostoma* sp., *Scaeva pyrastri, Sphaerophoria* spp., *Eupeodes meadii, Toxomerus* spp.	Bugg, pers. obs.; L. Linn, pers. comm.
Coyote brush *(Baccharis pilularis)*	Woody perennial: shrub, insectary hedgerow, field-side weed, chaparral plant	*Allograpta obliqua, Sphaerophoria* spp., *Scaeva pyrastri, Eupeodes volucris, Eupeodes* sp., *Melanostoma* sp., *Toxomerus* spp. *Allograpta exotica*	Bugg, pers. obs. W. E. Chaney, pers. obs.
Dhani-ya coriander *(Coriandrum sativum* 'Dhani-ya')	Herbaceous annual, culinary herb or spice, insectary plant	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
English Thyme *(Thymus vulgaris)*	Short-lived perennial broadleaf, culinary herb	*Allograpta exotica, Allograpta obliqua, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Holly-leaved cherry *(Prunus ilicifolia)*	Woody perennial: shrub/tree, insectary hedgerow, chaparral plant	*Allograpta obliqua, Sphaerophoria* spp., *Scaeva pyrastri, Eupeodes volucris, Eupeodes* sp., *Melanostoma* sp., *Toxomerus* spp.	Bugg, pers. obs.
Italian oregano *(Origanum vulgare)*	Perennial broadleaf, culinary herb	*Allograpta obliqua, Platycheirus stegnus Sphaerophoria sulphuripes, Toxomerus marginatus, Syrphus opinator*	W. E. Chaney, pers. obs.
NitroPersian Clover *(Trifolium resupinatum)*	Winter annual cover crop, insectary plant	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Painted sage *(Salvia horminum)*	Annual broadleaf, cut flower	*Allograpta obliqua, Sphaerophoria sulphuripes, Syrphus opinator Toxomerus marginatus*	W. E. Chaney, pers. obs.
Soapbark tree *(Quillaja saponaria)*	Woody perennial: tree, insectary hedgerow	*Scaeva pyrastri, Eupeodes volucris, Eupeodes* sp., *Melanostoma* sp.	Bugg 1987
Sweet alyssum *(Lobularia maritima)*	Herbaceous broadleaf annual, insectary plant	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Sweet Fennel *(Foeniculum vulgare* var. *dulce)*	Annual culinary vegetable or perennial spice	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Tansy phacelia *(Phacelia tanacetifolia)*	Herbaceous broadleaf winter annual, cover crop, insectary plant	*Allograpta exotica, Allograpta obliqua, Eupeodes americanus, Platycheirus stegnus, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus, Toxomerus occidentalis*	W. E. Chaney, pers. obs.
Tansy phacelia *(Phacelia tanacetifolia)* and white mustard *(Sinapis alba)*	Herbaceous broadleaf winter annual, cover crop, insectary plant	*Episyrphus balteatus, Melanostoma mellinum, Eupeodes corollae, Sphaerophoria mentastri group, Sphaerophoria scripta, Syrphus ribesii*	Klinger 1987
Toothpick ammi *(Ammi visnaga)*	Herbaceous broadleaf summer annual, insectary plant, field-side weed	*Allograpta obliqua, Sphaerophoria* spp., *Paragus tibialis, Scaeva pyrastri, Eupeodes volucris, Eupeodes* sp., *Melanostoma* sp.	Bugg and Wilson 1989
White Yarrow *(Achillea millefolium)*	Herbaceous broadleaf perennial, insectary plant	*Allograpta obliqua, Sphaerophoria sulphuripes, Syrphus opinator, Toxomerus marginatus*	W. E. Chaney, pers. obs.
Wild buckwheats *(Eriogonum* spp.)	Woody perennial: shrub, insectary hedgerow, chaparral plant	*Allograpta obliqua, Eupeodes volucris, Eupeodes* spp., *Melanostoma* sp., *Scaeva pyrastri, Sphaerophoria* spp., *Paragus tibialis, Toxomerus* spp.	Bugg, pers. obs.; Bugg and Heidler 1979; Swisher 1979

far as 200 m from strips of flowering phacelia. Long et al. (1998) used rubidium labeling of hedgerow plants to document the use of nectar and dispersal of beneficial parasitic and predatory insects, including aphidophagous flower flies (*Toxomerus* spp.), into adjoining fields. It is not known how annual in-field herbaceous insectary plants differ from perennial insectary hedgerows in terms of their effects on flower flies. It is clear that lines of trees, even with gaps, limit field-to-field dispersal of adult syrphids (Wratten et al. 2003), implying that insectary plantings on one side of a windbreak may confer only reduced benefits on the other side.

Landscape-scale studies of syrphids are still scarce (Fig. 41). Kleijn and Van Langevelde (2006) in the Netherlands reported that species richness of syrphids was significantly related to the abundance of flowers and the abundance of seminatural habitat within 500 to 1000 m and that flower abundance had positive effects only in areas with much seminatural habitat. This suggests that small stands of herbaceous insectary plants may not be enough by themselves to sustain high diversities of syrphids on agricultural lands.

Aphid Parasitoids

Several species of tiny parasitic wasps insert (oviposit) their eggs into aphid nymphs. Larvae emerge from these eggs and eat the aphid from the inside. These parasites include *Diaretiella rapae,* a braconid wasp that attacks cabbage aphid *(Brevicoryne brassicae)* and green peach aphid *(Myzus persicae).* Other groups of parasitoids include *Lysiphlebus* spp., *Aphelinus* spp., *Aphidius* spp., and *Praon* spp. These species may also build up on cereal aphids and disperse to other crops when cereals mature or are plowed down or when aphid populations crash. In Spain, where it is apparently native, lettuce aphid is attacked by *Aphidius hieraciorum* (the most abundant parasite in spring-grown lettuce), *Aphidius ervi,* and *Aphidius colemani* (the most abundant parasite in fall-grown lettuce) (Nebreda, Michelena, and Fereres 2005). We in California may not yet have the most effective forms of these parasites. In the same study, none of the important parasites of lettuce pest aphids was found on aphids associated with common field-side weeds (*Sonchus oleraceus, Brassica nigra, Silybum marianum, Senecio vulgaris,* and *Avena* spp.) (Nebreda, Michelena, and Fereres 2005).

Aphid Pathogens

Pathogens that attack aphids include fungi (Fig. 42) such as *Pandora neoaphidis, Beauveria bassiana, Zoophthora phalloides, Conidiobolus obscurus,* and *Entomophthora planchoniana,* which are important in the fog belt and can quickly reduce heavy aphid infestations. The last of these fungi appears as a white to pinkish growth on aphids and is easily distinguished from the dark, sooty mildew that colonizes the honeydew excreted by aphids.

Figure 41. Organic romaine lettuce field with adjoining foothills featuring annual grassland and chaparral vegetation.

Figure 42. Entomopathogenic fungi commonly infect lettuce aphids.

Pest Management in Organic versus Conventional Lettuce Production

Intercropping lettuce with insectary plants to attract natural enemies is standard practice among successful growers of organic lettuce on California's Central Coast, suggesting that the practice is economically viable given the current price premiums for organically grown lettuce. Conventional lettuce growers, however, do not take a formal approach to enhancing natural enemies or biological control in the suppression of lettuce aphid *(Nasonovia ribisnigri).*

This is probably because *N. ribisnigri* is not a good candidate for integrated control (that is, control combining both insecticides and natural enemies). There are no selective insecticides available that suppress aphids but not their natural enemies. Also, *N. ribisnigri* colonizes the innermost leaves of the lettuce head where contact insecticides are not effective and where systemic insecticides such as neonicotinoids have limited efficacy against high infestations. Conventional growers must therefore suppress incipient *N. ribisnigri* populations before they become well established. This pre-emptive approach with the aphids works against natural enemies, as well. By contrast, organic growers allow the aphid populations to become established so that syrphid populations will follow. Syrphid larvae usually constrain aphid populations to levels that produce minimal aphids and exuviae, quite a contrast to experimental situations in which syrphids are excluded. Nevertheless, it is still too risky for conventional growers to depend on natural enemies for aphid management, because even the low levels of aphids sometimes left by syrphids are unacceptable for conventional produce.

Although it is tempting to look for incremental changes toward a desired goal, such as a gradual reduction of insecticide use, grower behavior is largely determined by the pest management tools that are available and by legislation related to pesticide use. For this reason, shifts in behavior can sometimes be sudden rather than gradual. If conventional insecticides were withdrawn through regulation, the organic alternatives appear ready for more widespread adoption.

Other natural enemies may contribute to aphid mortality, but syrphid fly larvae make it possible to produce organic lettuce on a large scale, year-round. Therefore, organic growers should focus on measures that enhance the activity of syrphid flies and avoid other interference with syrphid fly activity. The application of spinosad for leafminer or worm control in organic lettuce does interfere with syrphid activity. In addition, growing aphid-susceptible lettuce without insectaries is not advised in areas where natural flowering vegetation is not abundant. Although we do not have hard data to prove this, the authors believe that concentrated stands of insectaries are probably more effective for enhancing syrphid activity than are individual insectary plants scattered through the field, an approach that is practiced by some growers. If broad-spectrum insecticides become less available for aphid management in lettuce, these guidelines may be useful to conventional growers as well as organic growers.

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